ISLAND FOX MONITORING AND DEMOGRAPHY ON SAN NICOLAS ISLAND–2009

FINAL REPORT

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Prepared For

NAVAIR Ranges Sustainability Office, Code 52F00ME, Point Mugu, California

AND

Naval Facilities Engineering Command, Southwest
San Diego, California
Agreement No. N62473-07-2-0018

March 2010

Recommended citation:

Hudgens, B. R. and D. K. Garcelon. 2010. Island Fox Monitoring and Demography on San Nicolas Island–2009. Unpublished report *prepared by* the Institute for Wildlife Studies, Arcata, California. 34 pp.

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EXECUTIVE SUMMARY

This report summarizes annual monitoring of island fox (*Urocyon littoralis*) on San Nicolas Island. The island fox is listed as threatened by the state of California (California Department of Fish and Game 1987), and the subspecies occurring on San Miguel, Santa Rosa, Santa Cruz, and Santa Catalina islands are federally listed as endangered. The San Nicolas Island fox is believed to be particularly susceptible to disease due to its high densities and low genetic diversity.

Since 2000 the U.S. Navy has supported annual monitoring of fox population size and demographic rates. From 2000 through 2009 that monitoring has been conducted by the Institute for Wildlife Studies (IWS). IWS has trapped and marked foxes on three long-term study grids situated in the major habitats comprising the island (inland dunes, desert scrub and grassland) and covering approximately 18% of the island area. As in previous years, there was substantial variation in fox numbers among the grids, with the highest capture success (83.1%), numbers of adult foxes captured (76), and estimated population size (80) occurring on the westernmost grid (Redeye) and lowest (25.6% capture success, 21 adults captured, estimated population size of 23) on the westernmost grid (Skyline). Fox numbers increased on Redeye and Tuft's grids and declined on Skyline grid in 2009. There was little difference in the total number of adults captured on all three grids. We again used two methods to estimate grid-specific fox densities, one using population estimates from mark-recapture analysis and mean-maximum distance moved of recaptured animals, and another using spatially explicit mark-recapture methods. The latter method yielded lower density estimates which were consistent with what would be expected from previous home-range studies.

Adult and juvenile apparent survivorships from 2008-2009(73% and 80%, respectively) were similar to mean annual survivorship of each age class over the past 10 years. Productivity was low in 2009; only 12 pups were captured and the majority of these were captured on Skyline grid, which supported the lowest numbers of adult females.

We again tested foxes for recent exposure to three canine pathogens and documented the presence of canine distemper (7% prevalence), canine adenovirus (58% prevalence) and canine parvovirus (16% prevalence). We noted a drop in the prevalence of distemper, potentially indicating that vaccination efforts are impacting nonvirulent native strains of this virus. Continued high prevalence of adenovirus indicates that this pathogen may be enzootic in the San Nicolas island fox.

We advocate continued monitoring of island fox population dynamics and survivorship to provide for the early detection of novel threats, such as an epidemic. To this end, we recommend that annual monitoring efforts be supplemented with frequent (e.g., daily) survival monitoring of a subset of foxes, and continued vaccination against canine distemper and rabies. We also recommend directed studies on island fox ecology on San Nicolas Island to better understand what drives spatial variation in fox densities and spatial-temporal variation in fox productivity.

INTRODUCTION and BACKGROUND

The island fox (*Urocyon littoralis*) is California's only endemic carnivore, with a range limited to six of the eight California Channel Islands (Moore and Collins 1995). Despite its small size—it is the smallest fox species in the United States—it is the largest native terrestrial mammal found on the California Channel Islands. Morphological and molecular studies (Collins 1982, 1993; Gilbert *et al.* 1990, Wayne *et al.* 1991, Goldstein *et al.* 1999) justify the current classification of the island fox as a separate species from the mainland gray fox (*U. cinereoargenteus*; Wilson and Reeder 1993) and support the classification of a separate subspecies for each island (Hall 1981, Moore and Collins 1995). The island fox is listed as threatened by the state of California (California Department of Fish and Game 1987), and the subspecies occurring on San Miguel, Santa Rosa, Santa Cruz, and Santa Catalina islands are federally listed as endangered (Federal Register: Volume 69, Number 44, Pages 10335–10353).

In early 2000, foxes on San Nicolas Island, California (*U. l. dickeyi*) and those on San Clemente Island, California (*U. l. clemente*) were considered to be the only subspecies maintaining viable populations (Suckling and Garcelon 2000). The four remaining subspecies suffered marked declines in the mid to late 1990s. The subspecies on all three northern California Channel Islands (Santa Cruz, San Miguel, and Santa Rosa) were in imminent danger of extinction owing to predation by golden eagles (*Aquila chrysaetos*; Roemer *et al.* 2001) and the Santa Catalina Island subspecies, declined from an estimated 1300 in 1989–90 (Roemer *et al.* 1994) to about 100 as a result of an outbreak of canine distemper virus that swept through the population in 1999 (Timm *et al.* 2000). Fortunately, captive breeding programs on all four islands have been successful, and releases of captive-born foxes to the wild began in 2004. Island-wide trapping results in 2004 indicated that both subpopulations on Santa Catalina Island had reached the recovery goal set by Kohlmann *et al.* (2003, 2005) of at least 150 individuals in each subpopulation. Based on the trapping results, the subpopulations were considered recovered and a decision was made to close the captive breeding facility and release all captives to the wild.

The aforementioned declines of island fox subspecies emphasize the importance of monitoring population parameters of the San Nicolas Island subspecies. In the summer of 2000, the Institute for Wildlife Studies (IWS) began a fox-monitoring program on San Nicolas Island by establishing three capture-recapture trapping grids to evaluate the current status and demography of the subspecies and to monitor changes in population parameters. Trapping on the grids has been repeated each year since 2000 (Juola *et al.* 2002, Schmidt and Garcelon 2003, 2004, Garcelon and Schmidt 2005, Schmidt *et al.* 2006, 2007) and this report describes results for the 2009 trapping session. Where appropriate, comparisons are made with the results from the nine previous years of monitoring.

STUDY AREA

San Nicolas Island is the westernmost of the four southern California Channel Islands (Fig. 1). San Nicolas has been owned and operated by the United States Navy since 1933 and is closed to the public. At approximately 98 km from coastal Ventura County, California, it is the farthest of the eight California Channel Islands from the mainland. The 58-km^2 island is approximately 13 km long and 5.5 km wide with elevation ranging from sea level to 278 m. It is the fourth smallest Channel Island, larger only than San Miguel, Santa Barbara, and Anacapa islands. The island is roughly a plateau, with arroyos cutting down to the shoreline. The island is composed primarily of coastal scrub habitat (42% of island area), barren areas (24%), and grassland habitat (12%) (Halverson *et al.* 1996). From west to east, the sampling grids (Fig. 2&3) are dominated by coastal scrub and inland dune habitats (Redeye grid), coastal scrub (Tuft's grid), and grassland and coastal scrub (Skyline grid). The combined area (*i.e.*, the area created by connecting the outer trap locations of each grid) of the three grids was 6.7 km^2 or 11.6% of the total island area. The combined effective trap area (see Methods section for definition) for the grids in 2006 was 10.6 km^2 or approximately 18% of the total island area (Fig. 3). The Tuft's grid contains the greatest density of coyote brush (*Baccharis pilularis*) and coast goldenbush (*Isocoma menziesii*) and both the Tuft's and Redeye grids contained high densities of *Lupinus* and *Astragalus* species and the

exotic sea fig or ice plant (*Carpobrotus chilensis*), which foxes are known to consume.

Fig. 1. San Nicolas Island, California viewed from the west (left) and from the north (right).

METHODS

Trapping and Handling

Foxes were trapped on the same three rectangular demography grids (Tuft's, Skyline and Redeye grids;

Fig. 2 & 3; Table 1; Appendix A) used since the start of the fox monitoring program in 2000. Traps (23 x 23 x 66 cm box traps, Tomahawk Live Trap Co., Tomahawk, WI) on all three grids were placed at 250-m intervals and opened for six consecutive nights. Traps were baited with dry cat food, and a loganberry paste attractant (On Target A.D.C., Cortland, IL). Traps were covered with burlap and vegetation to provide protection from the sun and wind, and the bottoms were lined with grass to cover the metal of the trap and as bedding material for captured foxes. Traps contained "bite bars" (20-cm section of 1.3-cm-diameter polypropylene tubing attached to the inside of the trap with flexible wire) that captured animals could bite without damaging their teeth. As foxes routinely dig under traps to retrieve the bait when it falls through the mesh floor, a piece of plastic was placed behind the treadle to prevent it from falling out of the trap.

Data recorded on the first capture of each fox included date, grid name, trap number, passive integrated transponder (PIT) tag number (used as a unique identifier), sex, weight (to nearest 0.025 kg), ectoparasites (fleas, ticks, lice, ear mites) present, eye condition, reproductive condition and tooth condition. If an animal was not previously tagged, a subcutaneous PIT tag was inserted between and just anterior to the scapulae using a single-use sterile needle and syringe. Foxes were aged as pups or into one of four adult age classes (age class 1 through age class 4) according to tooth eruption and dentin exposure patterns relating to wear on the first upper molar (Wood 1958, Collins 1993). The relationship between age class and true age is depicted in Appendix B. Foxes were also assigned a relative body condition (1-5), with a 1 being a skinny animal with little or no body fat and a 5 being obese. We also noted any injuries or physical abnormalities, including those that appeared to have been related to the animal's capture.

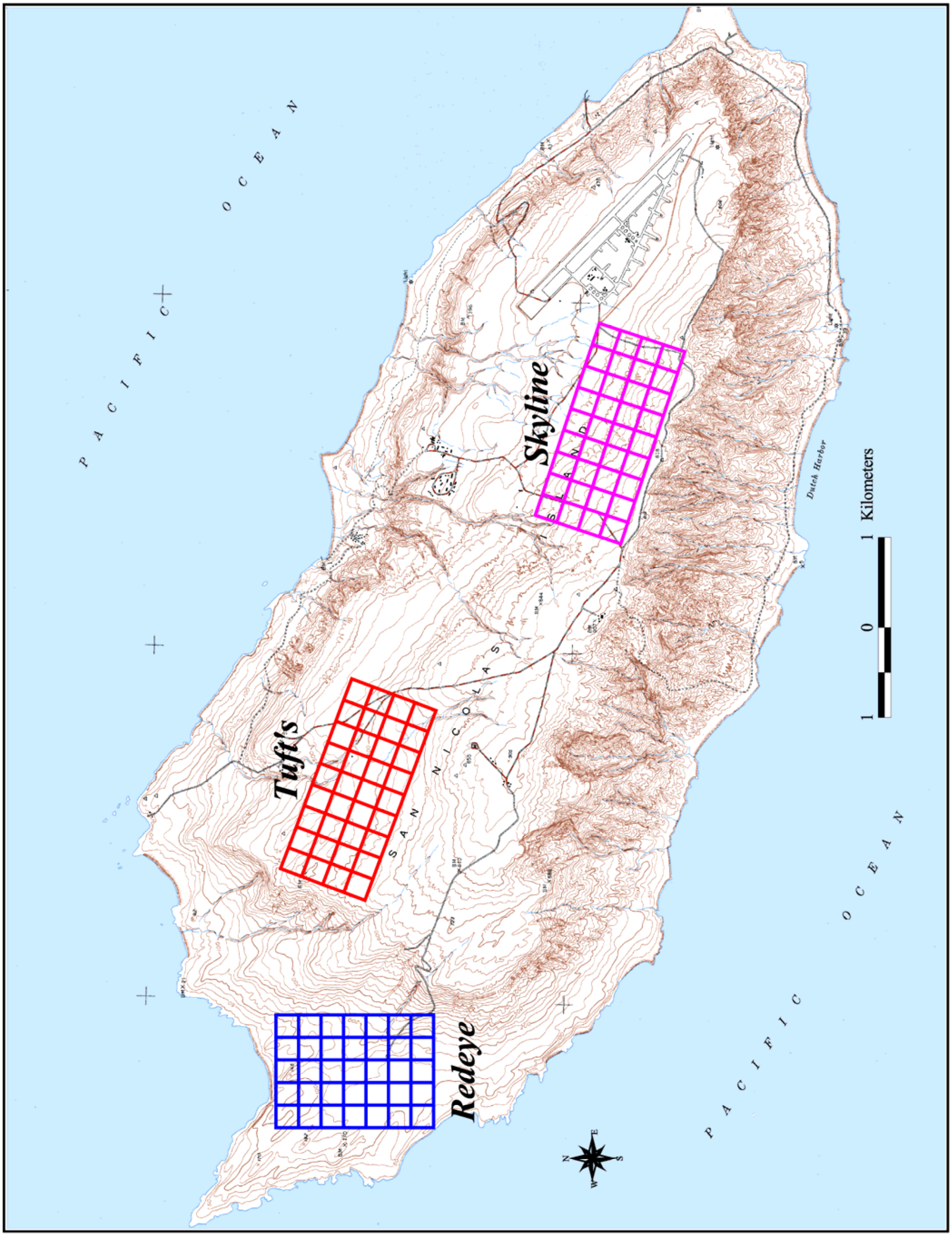


Figure 2. Island fox demography grids, San Nicolas Island, California.

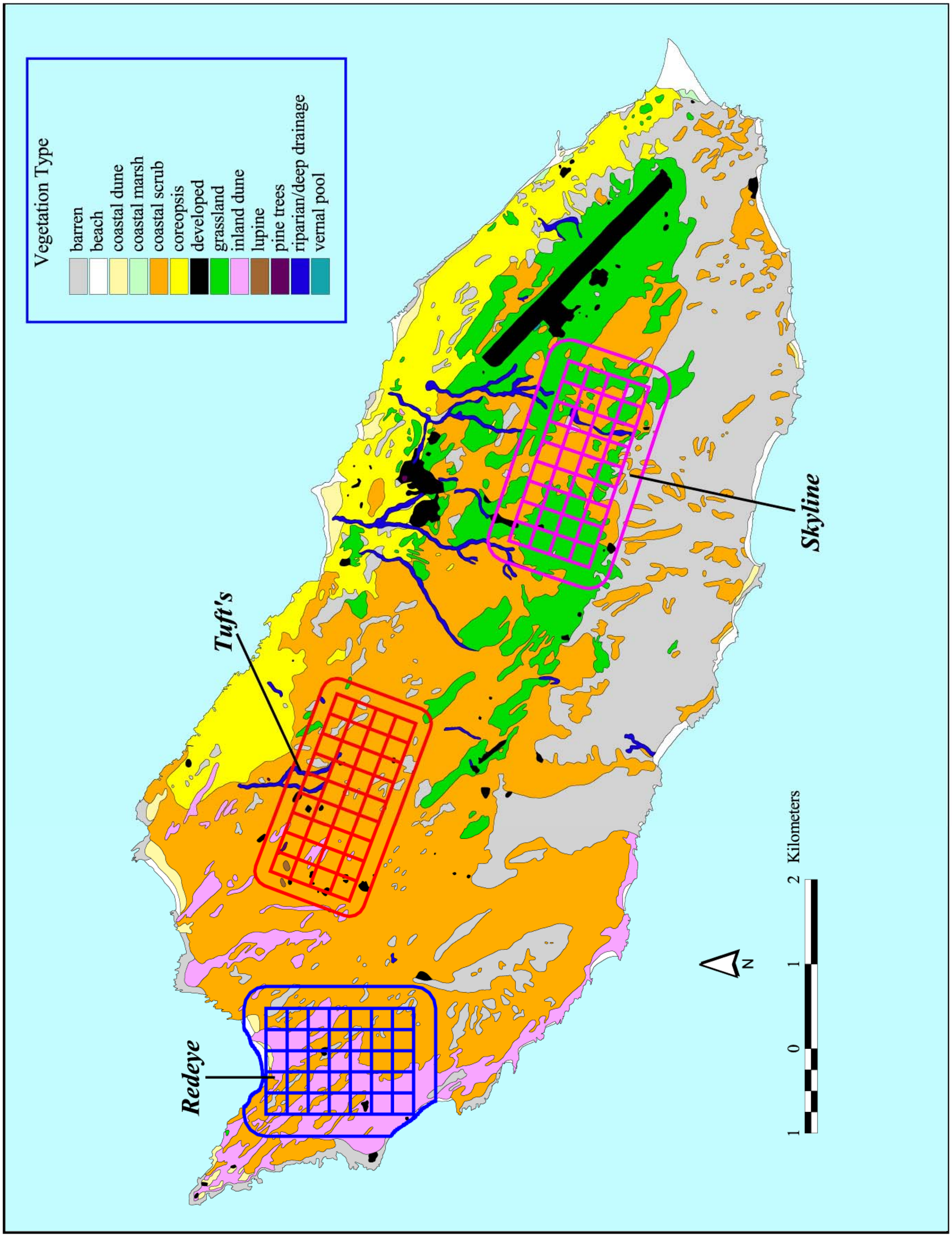


Figure 3. Island fox demography grid effective trap areas (polygon surrounding each grid), San Nicolas Island, California.

Checking the teeth and assigning an age class to a captured fox.

A subset of foxes captured on all grids were vaccinated against canine distemper virus and rabies virus. Ear mites were collected from a sample of the foxes captured to aid in an inter-island study on the effect of these ectoparasites on fox health. Up to 10 ml of blood was collected from the femoral vein or artery or jugular vein of select foxes for genetic and serologic analysis, and feces were collected when available. Serum was extracted from whole blood after centrifugation using a sterile pipette. Serum samples were split into 1 ml aliquots, each of which were placed in a 1.8-ml cryovial prior to freezing.

Analyses

Fox health

We determined if there were significant differences in mean body weight by sex or grid using analysis of variance. Except as noted, all analyses were conducted with SAS (SAS Institute, Inc., Cary, NC, USA 2001) software. For all tests of significance, we used an alpha of 0.05.

Population Size, Density, Growth Rate, on Demography Grids

We used Pollock's robust design (Pollock 1982, Pollock *et al.* 1990, Kendall *et al.* 1995, Kendall 2001) within program MARK (version 5.1, White and Burnham 1999) to estimate adult fox population size (> age class 0) on each demography grid from adult capture histories on that grid. Adult capture histories represent the trapping days on which an animal was captured during grid trapping. The analysis assumes that fox populations are demographically closed (*i.e.*, no significant natality, mortality, immigration, or emigration occurs during the trap period) within a trapping session but allows for open populations between years.

We estimated adult population size using the Huggins estimator. We ran several models which differed in their assumptions about how daily capture and recapture probabilities, annual temporary dispersal, and annual survival probabilities varied from year to year and among grids. Based on previous analyses, we assumed that daily capture and recapture rates were constant within a trapping session, but tested models allowing these parameters to vary from year to year and by grid. Temporary dispersal parameters account for animals that occasionally inhabit a grid, but may not be present on the grid during a trapping session (e.g., an animal whose home range shifts from year to year near the edge of the grid). Because there were few occasions of an animal trapped one year, missed the subsequent year and later trapped on the same grid, we limited analyses to models which had constant emigration and return rates across grids and years, and models which allowed emigration rates to vary by grid. Finally, we tested models for which adult survival varied by grid, by year, or both.

We estimated population size (and confidence intervals) as the weighted average of the models receiving the most support from the data as determined using AICc (Akaike's Information Criteria corrected for small samples) weights reported by program MARK. AICc weights represent the probability that a given model is the best approximation of the true description of the data among those models tested. This method of model averaging accounts for both uncertainty in parameter estimates from a given model and uncertainty about which model best fits the data (*i.e.*, best describes the biological processes producing the data).

For each grid we used the density estimator, D=N/A, where N is the estimate of the grid population size (from program MARK) and A is the area influenced by the trap grid. This area was

Table 1. Island fox demography grid descriptions, San Nicolas Island, California.

Grid	Years trapped	No. of traps	Grid configuration	Inter-trap distance (m)	No. of nights trapped each year	Perimeter area (km^2)[a]	Percent of total island area[b]	Primary vegetation types within grid perimeter (within effective trap area for 2006)[c]
Redeye	2000–2009	48	6 x 8	250	6 (5 in 2007)	2.19	3.8	47% (42%) inland dune; 46% (49%) coastal scrub; 5% (5%) barren
Skyline	2000–2009	50	5 x 10	250	6 (5 in 2007)	2.25	3.9	52% (52%) grassland; 43% (38%) coastal scrub; 3% (7%) barren
Tuft's	2000–2009	50	5 x 10	250	6 (5 in 2007)	2.25	3.9	90% (89%) coastal scrub; 4% (4%) barren; 2% (2%) inland dune

[a]Represents the area created by connecting the outer trap stations.
[b]For grid perimeter only, not the effective trap area.
[c]Percentages are rounded to the nearest whole number. Effective trap area is the sum of the grid perimeter area and the strip surrounding the grid that is likely influenced by the traps.
[d]See Fig. 2 and Fig. 3 for grid locations and Fig. 3 for effective trap area polygons.

the sum of the grid perimeter area and an additional strip around the grid perimeter; the strip width was calculated from an estimate of the mean maximum distance foxes moved (MMDM; Wilson and Anderson 1985) between captures that was generated by program DENSITY. Pups (age class 0) were excluded from estimates of population size and density due to their close association with adults––the relatively short movements of the less mobile pups could decrease the MMDM, resulting in a smaller area of influence and inflated density estimates.

This year we again used program DENSITY (Efford et al. 2004) as a second method of estimating island fox population density for each of the grids. Program DENSITY applies spatially explicit capture-recapture, using the locations where each animal is trapped to fit a spatial model of detection. The resulting estimate of population density are unbiased by edge effects and incomplete detection. We used the maximum likelihood option within program DENSITY to the spatial detection model.

Population growth rates (λ) for the demography grids were calculated as $\lambda = N_{t+1} / N_t$, where N_t is population size (or density in this case) at time t. Thus, $\lambda < 1$ indicates the population is declining, $\lambda > 1$ indicates the population is increasing and $\lambda = 1$ indicates a stable population. To provide the Navy with a long-term prospective to the status and trends of the fox population we have added data collected by the Institute for Wildlife Studies from 2000 through 2008.

<u>Apparent Survivorship</u>

We also used program MARK to estimate annual survivorship. Because mark-recapture data cannot distinguish between mortalities and permanent dispersal from trapped areas, estimated survival rates are really apparent survivorship, i.e., the probability that an animal captured on a grid neither dies nor permanently disperses to untrapped areas in the following year. Hereafter, we will refer to apparent survival simply as survival. Our analysis this year focused on assessing what biological factors (e.g., age, gender) are associated with variation in fox survivorship. Models were evaluated in program MARK using the Huggins estimator for data taken according to Pollock's robust design. To facilitate comparisons with previous years, we calculated survival estimates as an island-wide parameter. Since we were not interested in accommodating dispersal among

grids in these analyses, we did not use the multi-strata analysis. Instead, we combined capture histories for all animals captured on any of the grids. This simplified the model structure, facilitating analyses by sex and age-class, while still accounting for temporary emigration from trapped areas.

Our first steps were to reduce the possible number of different models describing different assumptions about capture and recapture probabilities, and temporary emigration from and return to trapping grids. Each fox was categorized as either captured first as a pup (age class 0) or first as an adult (age class 1-4). We then estimated parameter values for several models of survivorship, temporary emigration from and return to sampled areas, and probability of capture or recapture. We then determined the most parsimonious model of capture/recapture probabilities, assuming that survivorship varied by age class, gender, and year, and that dispersal varied by age. The most parsimonious model was judged as the model with the lowest corrected Akaike's Information Criterion (AICc) score that did not result in nonsensical parameter estimates (e.g., one with values <0 or >1 within the 95% confidence interval). The AICc score is calculated as the negative log-likelihood of a model given the data penalized by the number of parameters in the model (Akaike1973; see White and Burham 1999 and Johnson andOmland 2004 for reviews)
We tested models allowing capture and recapture probabilities to vary by age at first capture, sex, and year, and all combinations of these three variables. After determining the most parsimonious model for capture/recapture probabilities, we determined the most parsimonious model structure for temporary dispersal on and off grids assuming that survivorship varied by age class, gender and year, and capture and recapture probabilities varied by age at first capture and year (the best fit model from the analysis above). We began this process by varying assumptions about return probabilities to trapping grids, assuming that temporary emigration varied by age and sex. We then varied assumptions about emigration rates assuming constant return rates based on the results from our examination of return probabilities.

Finally, we varied assumptions about whether survivorship varied by age class, gender, and year. Unlike capture-recapture and return probabilities, there was not a single model of emigration probabilities that was clearly superior to other models (see below). We therefore assessed models of survivorship assuming the most parsimonious model for capture-recapture probabilities and return probabilities, and the top two models of emigration probabilities to ensure that conclusions about fox survivorship were robust to assumptions about temporary emigration.

In order to estimate survivorship for each year (2000–2009), we calculated a weighted average of the survivorship estimates from all models included in the top 95th percentile of AICc weights.

Testing for Exposure to Canine Diseases

We collected blood samples from 43 foxes to test for exposure to canine adenovirus (CAV), canine distemper (CDV) and canine parovirus (CPV). These viruses were selected due to their epidemic potential and possible fatal outcomes in susceptible individuals. These diseases were also selected because island foxes on San Clemente Island were monitored for exposure to these diseases in 2007 (Garcelon et al. 2008). Blood was collected in the field using veinapuncture and the sample was placed in a tube and allowed to clot. While in the field the blood was kept cool using ice packs. The sample was later separated by centrifugation and the serum pipetted off and frozen in cryotubes. The samples were sent for testing to the Animal Health Diagnostic Center at Cornell University in Ithaca, NY.

Island fox pup receiving an examination.

RESULTS

Capture Statistics

We captured 156 adult foxes (78M, 78F) and 12 pups (4M, 8F) a total of 431 times on three grids (Table 2). This was very similar to the totals from 2008, when 151 adults were captured 419 times. A total of 26 (16.7%) of the adults were captured on a grid for the first time in 2009. A large proportion of these (46%) were in the age-class one category. Capture success for the three grids averaged 52.8% (Table 2). Foxes were captured an average of 2.6 times. Only two foxes were captured on more than one grid during the sampling period. Two males, age classes 2 and 4, were captured on both Tuft's and Redeye grids. No feral cats were captured in 888 trap-nights.

Age structure varied across the three grids, with age classes 1 or 2 making up the largest proportion of adults for each grid (Fig 4). The relative age structure for Redeye was similar to that found in previous years, but in both Tuft's and Skyline grids, the proportion of individuals in age class 3 was relatively high and the proportion of individuals in age class 1 was relatively low (Fig. 5).

We obtained serum samples from 84 foxes (33 from Redeye, 33 Tuft's, 18 Skyline). We inoculated 76 foxes against canine distemper virus and 80 against rabies virus (Skyline 0, Tuft's 53, Redeye 27). We also removed 17 radio-collars from foxes that had been previously been part of a fox mortality study.

Physical Condition

In a general assessment of body condition (scale of 1-5, with 1 being thin and 5 being obese), 69.3% of the foxes examined were in average to good condition, and 15.7% were considered thin or in poor condition. The remaining 15.0% were considered in very good condition.

There was a significant difference in body weight of females among grids ($P = 0.032$; $F = 3.59$; $df = 2$), with the females on Tuft's having the lowest average body weights (Table 3). Weights of males also differed significantly among grids ($P = 0.022$; $F = 4.0$; $df = 2$), but there was no difference when just Tuft's and Redeye males were compared ($P = 0.108$; $F = 2.65$; $df = 1$). Adult males on the Skyline grid had the lowest average body weights (Table 3).

Fleas (*Pulex irritans*) were found on only 2 foxes (1.2%); no ticks or lice were found on any captured foxes.

Table 2. Island fox demography grid trapping results, 2009, San Nicolas Island, California (see Fig. 2 or 3 for grid locations).

Grid	Dates open	No. Trap-nights	No. Adult males	No. Adult females	Total No. adults	No. Male pups	No. Female pups	Total No. pups	Total No. captures[a]	Capture success (%)[b]
Redeye	8/15–8/20	288	40	37	77	2	0	2	226	83.1
Skyline	6/30–/05	300	9	12	21	2	5	7	74	25.6
Tuft's	8/08–8/13	300	29	29	58	0	3	3	131	51.2
		Total	78	78	156	4	8	12	431	52.8

[a]Includes recaptures.
[b]Calculated by dividing total number of captures by the number of trap-nights.

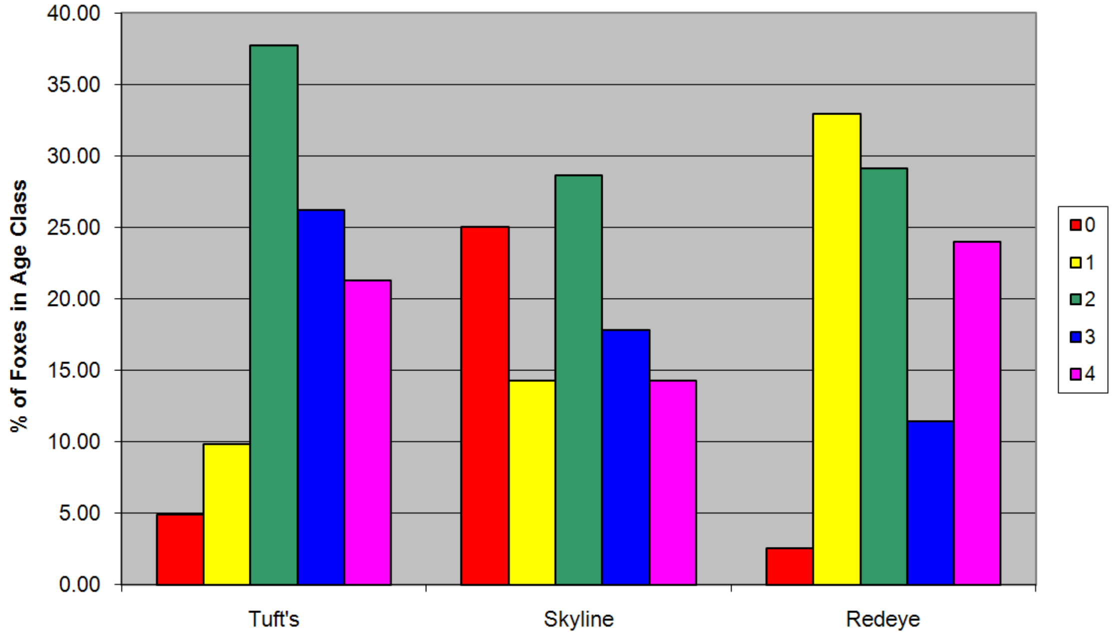


Fig. 4. Age class distribution by demography grid, 2009, San Nicolas Island, California.

Table 3. Mean weight (kg) of adult island foxes captured on grids, 2009, San Nicolas Island, California.

Grid	Sex	*n*	Mean	SD
Redeye	M	40	1.78	0.236
	F	37	1.65	0.231
Skyline	M	9	1.56	0.259
	F	12	1.64	0.302
Tuft's	M	29	1.70	0.178
	F	29	1.51	0.184
All foxes combined	M	78	1.72	0.227
	F	78	1.60	0.234

The most common physical "abnormalities" noted for the 168 foxes captured on grids in 2009 were minor cuts or abrasions (9.5%), matted or missing fur (8.3%) and ear notches or missing tips (8.3%)% (Table 4). and cuts, abrasions, and punctures injuries likely caused by intraspecific interactions. Two foxes had evidence of old fractures and one of a recent unhealed fracture. Six individuals (3.6%) broke one or more teeth while in a trap. However, we only inspected foxes thoroughly for trap-related injuries on their initial capture; therefore, it is possible that additional tooth breakage may have occurred upon subsequent recapture.

Table 4. Physical abnormalities of island foxes captured on grids, 2009, San Nicolas Island, California.

Physical "abnormality"	No. of foxes
Matted or missing fur	14
Minor cuts/abrasions	16
Partial missing ear(s)	14
Broken tooth (trap damage)	6
Lip injuries	10
Fractures	3

Productivity

Across all grids, 16 (20.8%; n = 77) of the females were either lactating or showed signs of having lactated this year. The pup to adult female ratio for all grids combined was 0.15:1 (12 pups captured, 78 adult females captured). Reproduction was concentrated on the Skyline grid, where seven pups and 12 adult females were captured, yielding a pup:adult female ration of 0.58:1.

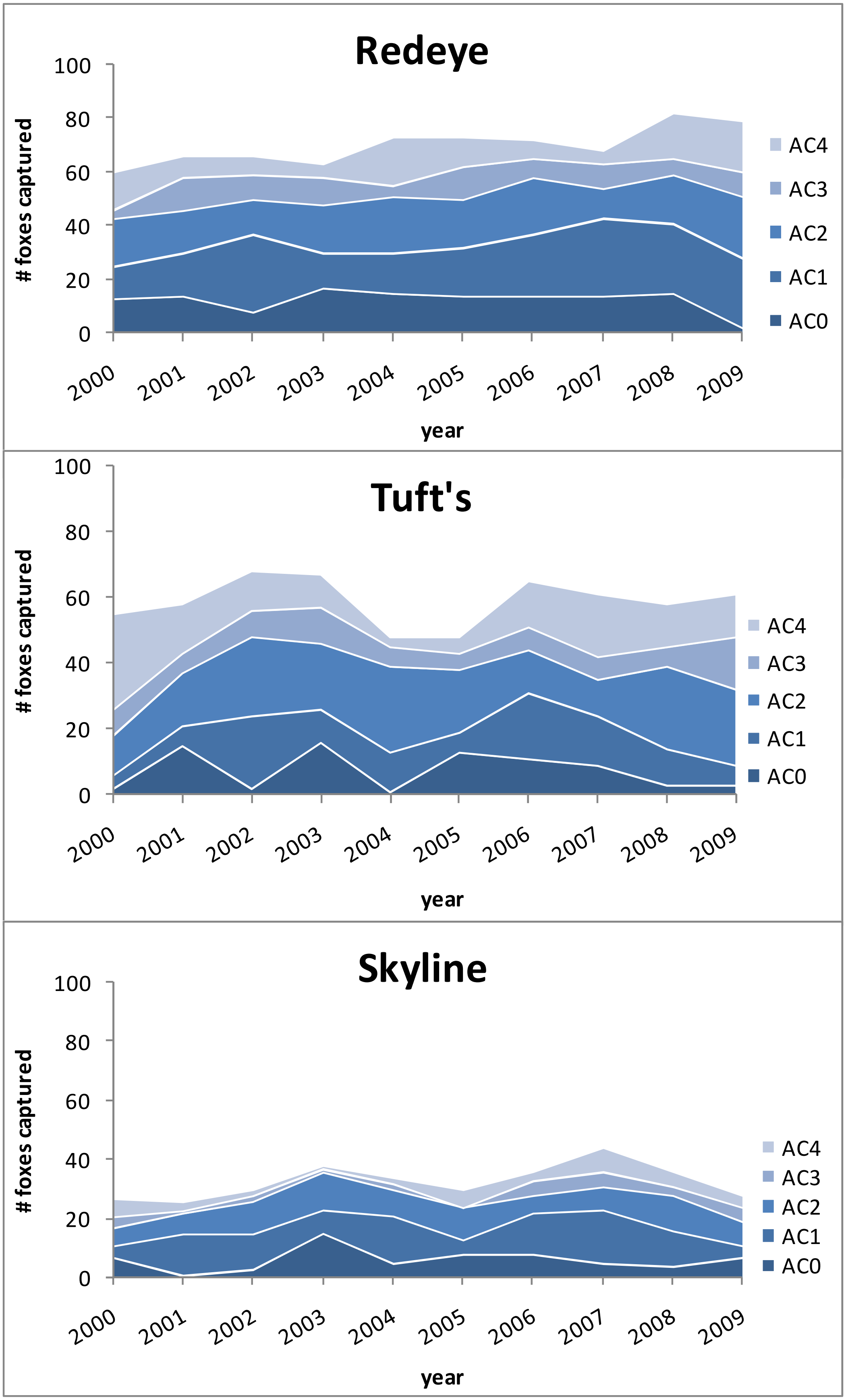


Fig. 5. Age class distribution by demography grid, 2000-2009, San Nicolas Island, California.

Serology

Many of the foxes captured had previously been vaccinated for CDV and therefore would have provided antibody results that would have been difficult to interpret. For the 43 serum samples submitted for testing from foxes with no previous vaccination history, 49% tested positive for CAV, 7% for CDV and 16% for CPV (Appendix C). Five (11.6%) of the foxes sampled had positive titers for two of the three canine viruses.

Movements

Between 2008 and 2009, four tagged foxes moved from Redeye to the Tuft's grid. These individuals were made up of 3 males and 1 female. As the grids are not a great distance apart, these may not have been permanent changes in home ranges. In fact, one fox that was mentioned described above having been caught on both Redeye and Tuft's during 2009, was captured on Redeye in 2008, so may actually occupy an area between the two grids.

Population Size, Density, Growth Rate, and Apparent Survivorship on Demography Grids

Adult fox population size estimates ranged from 23 on the Skyline grid to 80 on the Redeye grid (Table 5). Population size estimates for 2009 indicate that the number of adult foxes on the grids increased from 2008 for both Redeye and Tuft's, but decreased on Skyline for the second consecutive year (Fig. 6-8). The mean annual rate of adult population change (λ) for 2000–2008 was >1 for all grids (Fig. 6–8).

Density estimates using values from program MARK/MMDM ranged from 6.5 foxes/km^2 on the Skyline grid to 24.2 foxes/km^2 on the Redeye grid (Table 5). As in 2008, density estimates using program DENSITY provided lower values for all three grids, when compared to density calculated from program MARK, although there was overlap in the 95% confidence intervals of the estimates for Skyline and Tuft's grids from the two methods (Tables 5 & 6). The results for 2009 using program DENSITY were essentially the same as in 2008 for the Redeye grid, and slightly higher for the Tuft's grid. Fox density on the Skyline grid was less than half of the estimate from 2008, although the 95% confidence intervals still overlapped (Table 6).

The most parsimonious model for fox capture and recapture probabilities allowed these parameters to vary by year and by age at first capture, but not by gender (Table 7). The best fit dispersal models constrained both emigration and return rates to be constant across groups and time (Table 8). Models that incorporated different temporary emigration probabilities for male pups than other groups of foxes were also supported by the data, with male pups having a higher probability of emigrating than other foxes. Although there was support for models allowing temporary emigration rates to vary by age or by gender, inspection of parameter estimates generated from these models revealed no difference in estimates between all pups and all adults or between males and females.

The most highly supported model for fox survival did not vary by age class, gender or time (Table 9). There was some support in the data for survival differences between pups and adults, and very weak support for differences between males and females. Examination of yearly estimates of survival probabilities (Fig. 9) reveals that male and female survival track each other closely. There was remarkable consistency in adult survivorship from year to year at approximately 76% (95% CI=73%-79%) (Fig. 9a). Juvenile survivorship averaged 78% (95% CI=73%-82%) from 2000-2009, but annual estimates were less precise (i.e., had larger 95% confidence intervals) and exhibited greater fluctuations than adult survivorship, dipping to a low near 50% in 2004-2005 (Fig. 9b). Survivorship from 2008-2009 was within 3% of the 10 year average for both juveniles (80.3%; 95%CI=43%-95%) and adults (73%; 95% CI=59%-83%).

Table 5. Total number of adults captured, population estimates, effective trap area, and adult density estimates for the three demography grids, 2009, San Nicolas Island, California.

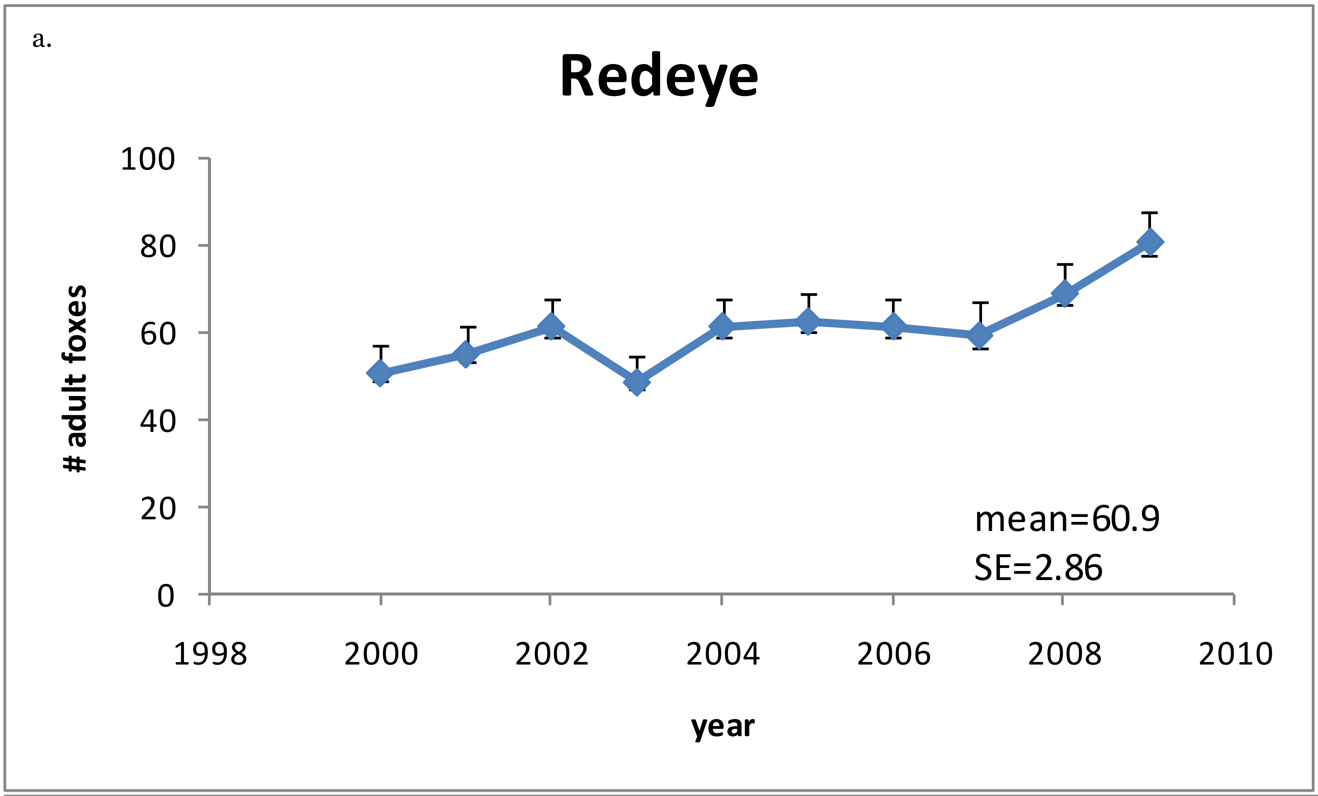
Grid[a]	No. Adults captu-red[b]	Population estimate	95% C. I.	Effec-tive trap area (km^2)	Density estimate (foxes/km^2) based on population es-timate[c]	Density estimate range based on 95% C.I. of population estimate (fox-es/km^2)[d]
Redeye	76	80	78–88	3.31	24.2	23.6-26.6
Skyline	21	23	22–29	3.53	6.5	6.2-8.2
Tuft's	58	67	62–77	3.81	17.6	16.3-20.2

[a]See Fig. 2 or Fig. 3 for grid locations.
[b]One fox was captured on both Skyline and Redeye grids.
[c]Calculated as population estimate/effective trap area.
[d]Range calculated as population estimate/effective trap area, using the upper and lower bounds of the 95% C. I. of the population estimate.

Table 6. Island fox density calculated for 2008 and 2009 using program DENSITY with maximum likelihood function.

Grid[a]	No. adults captured	Maximum likelihood density (foxes/km^2)	SE	95% C.I. of density estimate	λ
Redeye 2008	65	15.9	2.27	12.2-21.2	
Redeye 2009	76	15.4	2.02	11.9-19.8	0.97
Skyline 2008	32	7.3	1.63	4.7-11.2	
Skyline 2009	21	3.53	1.13	1.9-6.5	0.48
Tuft's 2008	55	11.5	1.98	8.2-16.1	
Tuft's 2009	58	13.16	1.96	9.8-17.6	1.14

[a]See Fig. 2 or Fig. 3 for grid locations.



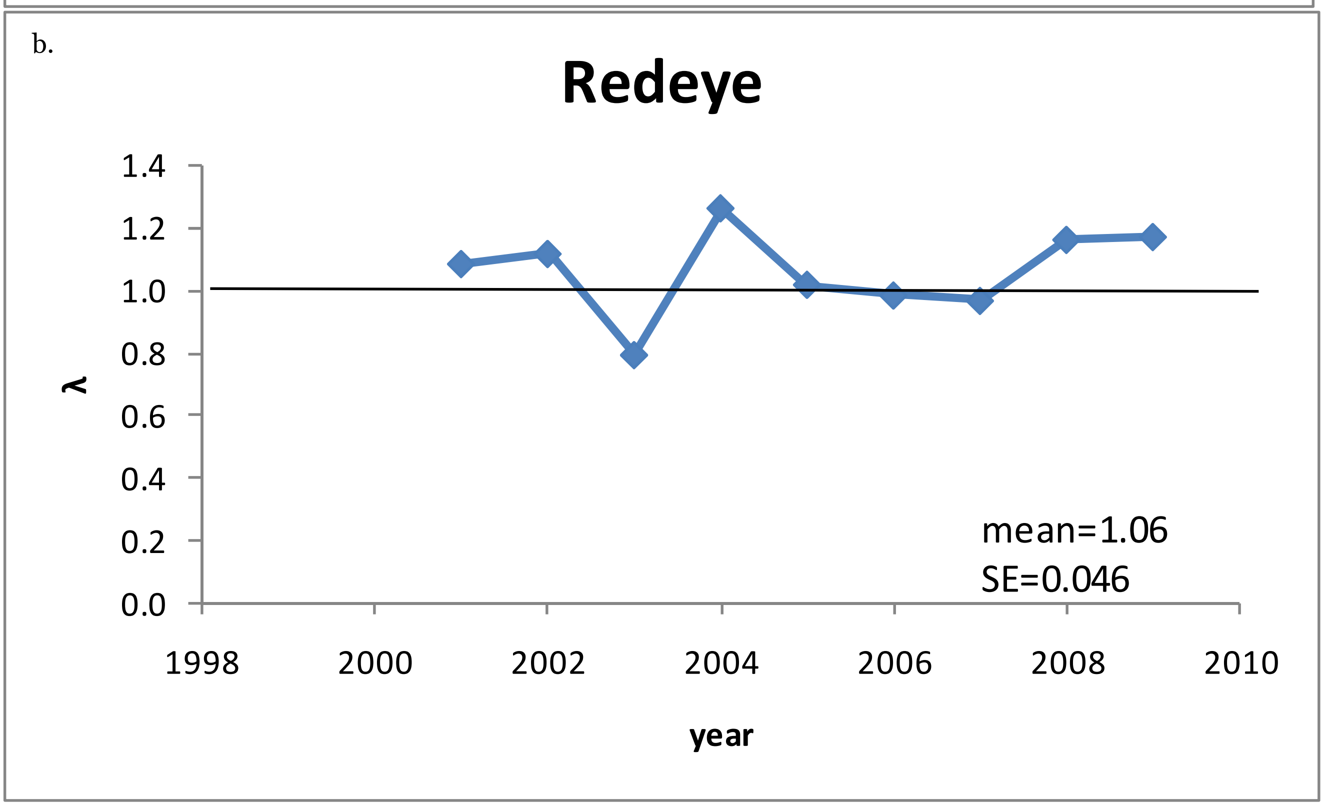


Fig. 6. Redeye grid (a) adult population size and (b) growth rate (λ) estimates 2000–2009, San Nicolas Island, California. Vertical lines represent 95% confidence intervals. A λ <1 indicates the population is declining and λ >1 indicates the population is increasing. A λ of 1 indicates a stable population (shown by horizontal line).

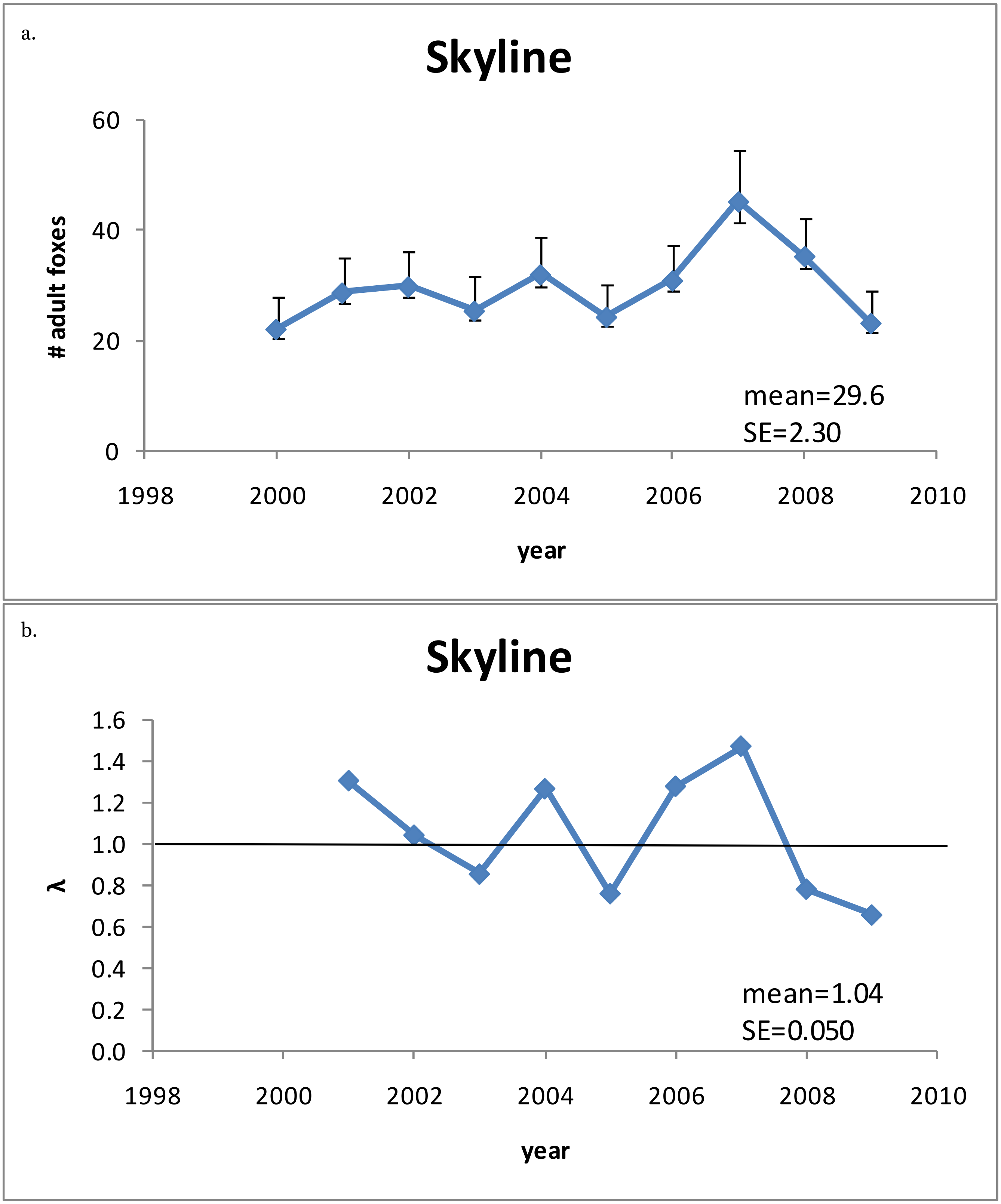


Fig. 7. Skyline grid (a) adult population size and (b) growth rate (λ) estimates 2000–2009, San Nicolas Island, California. Vertical lines represent 95% confidence intervals. A λ <1 indicates the population is declining and λ >1 indicates the population is increasing. A λ of 1 indicates a stable population (shown by horizontal line).

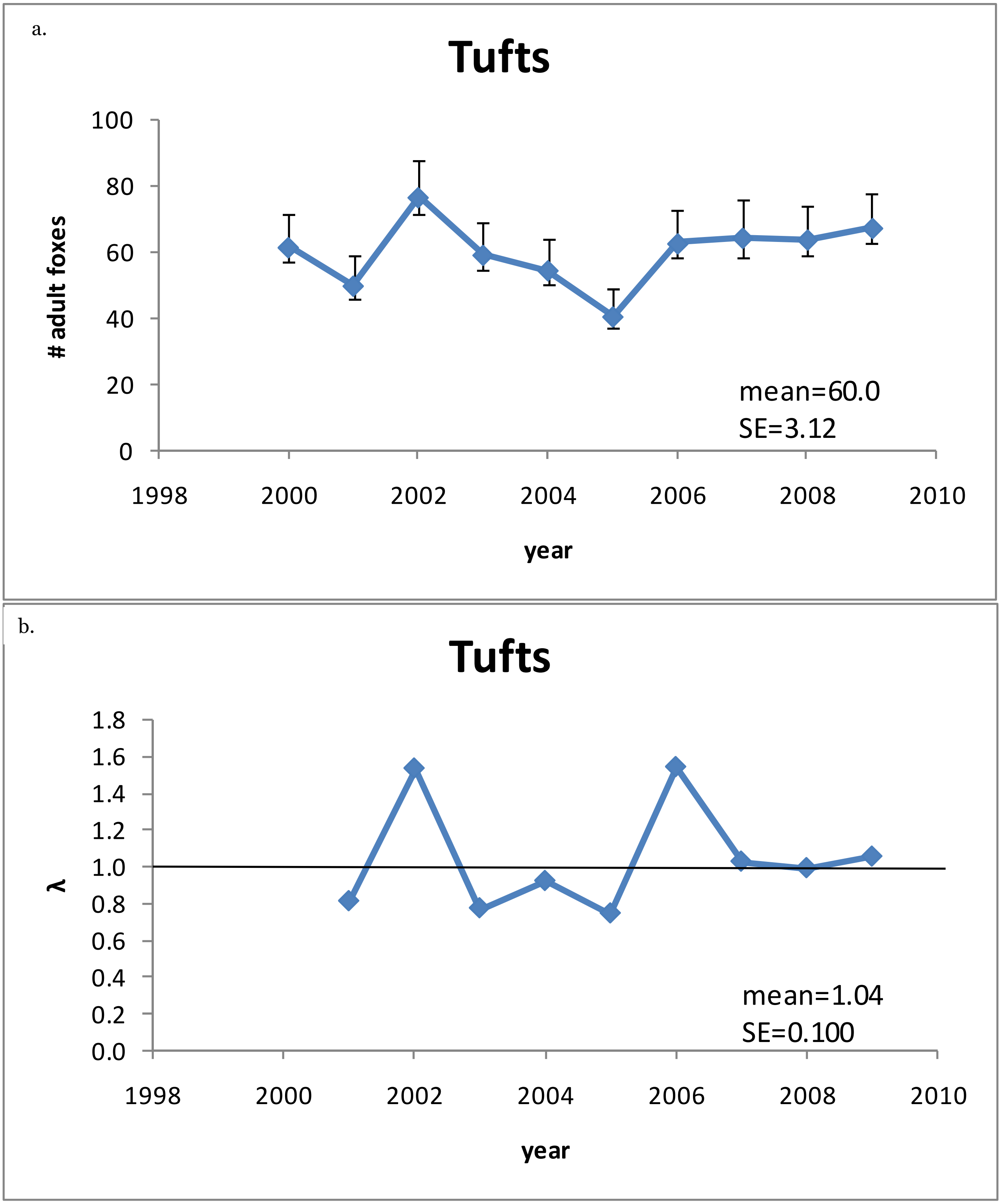


Fig. 8. Tuft's grid (a) adult population size and (b) growth rate (λ) estimates 2000–2009, San Nicolas Island, California. Vertical lines represent 95% confidence intervals. A λ <1 indicates the population is declining and λ >1 indicates the population is increasing. A λ of 1 indicates a stable population (shown by horizontal line).

Table 7. Model comparison for capture (c)-recapture (p) probabilities. For all models, survivorship was allowed to vary by age, sex and year, and temporary dispersal parameters were allowed to vary by age and sex.

Capture-Recapture Parameters:	AICc	Delta AICc[a]	AICc Weight[b]	Para-meters	Deviance
age class at first capture, year	30862.59	0	1.00	84	37557.01
age class at first capture, sex, year	30888.70	26.11	0.00	124	37500.98
year	30892.50	29.91	0.00	64	37627.68
sex, year	30933.12	70.53	0.00	84	37627.54
age class at first capture	31024.04	161.46	0.00	48	37791.68
age class at first capture, sex	31025.09	162.51	0.00	52	37784.63
sex	31040.00	177.41	0.00	48	37807.64

[a]Models differing by an AICc value greater than 2.0 are considered significantly different.
[b]AICc weight indicates the probability that the model is the best description of the data among the models tested.

Table 8. Model comparison for temporary emigration (e) and return (i) probabilities. For all models, survivorship was allowed to vary by age, gender and year, and capture-recapture parameters varied by age class at first capture and year.

Model	AICc	Delta AICc[a]	AICc Weight[b]	Para-meters	Deviance
e, i constant[c]	30851.84	0	0.36	78	37558.51
e male pups v others, i const	30853.07	1.24	0.19	79	37557.70
e by age class, i const	30853.61	1.77	0.15	79	37558.24
e male pups v others, i const	30853.80	1.96	0.13	79	37558.43
e by sex, i const	30853.87	2.03	0.13	79	37558.50
e,by age, sex, i const	30856.88	5.04	0.03	81	37557.43
e, by age class, sex i by sex	30858.92	7.08	0.01	82	37557.42
e,i by age class, sex[d]	30862.59	10.75	0.00	84	37557.01

[a]Models differing by an AICc value greater than 2.0 are considered significantly different.
[b]AICc weight indicates the probability that the model is the best description of the data among the models tested.
[c]const=parameter held constant across all groups and years
[d]Top model from Table 7.

Table 9. Model comparison for annual survival probabilities. For all models, temporary emigration and return probabilities were constant across groups and time, and capture-recapture parameters varied by age class at first capture and year.

Model	AICc	Delta AICc[a]	AICc Weight[b]	Parameters	Deviance
constant[c]	30816.01	0	0.33	43	37593.77
age class	30817.17	1.16	0.18	44	37592.90
sex	30818.03	2.02	0.12	44	37593.76
age class, sex	30821.13	5.11	0.03	46	37592.81
age class, year	30821.42	5.41	0.02	60	37564.73
sex, year	30831.90	15.88	0.00	60	37575.20
age class , sex, year[d]	30851.84	35.83	0.00	78	37558.51

[a]Models differing by an AICc value greater than 2.0 are considered significantly different.
[b]AICc weight indicates the probability that the model is the best description of the data among the models tested.
[c]const=parameter held constant across all groups and years
[d]Top model from Table 8.

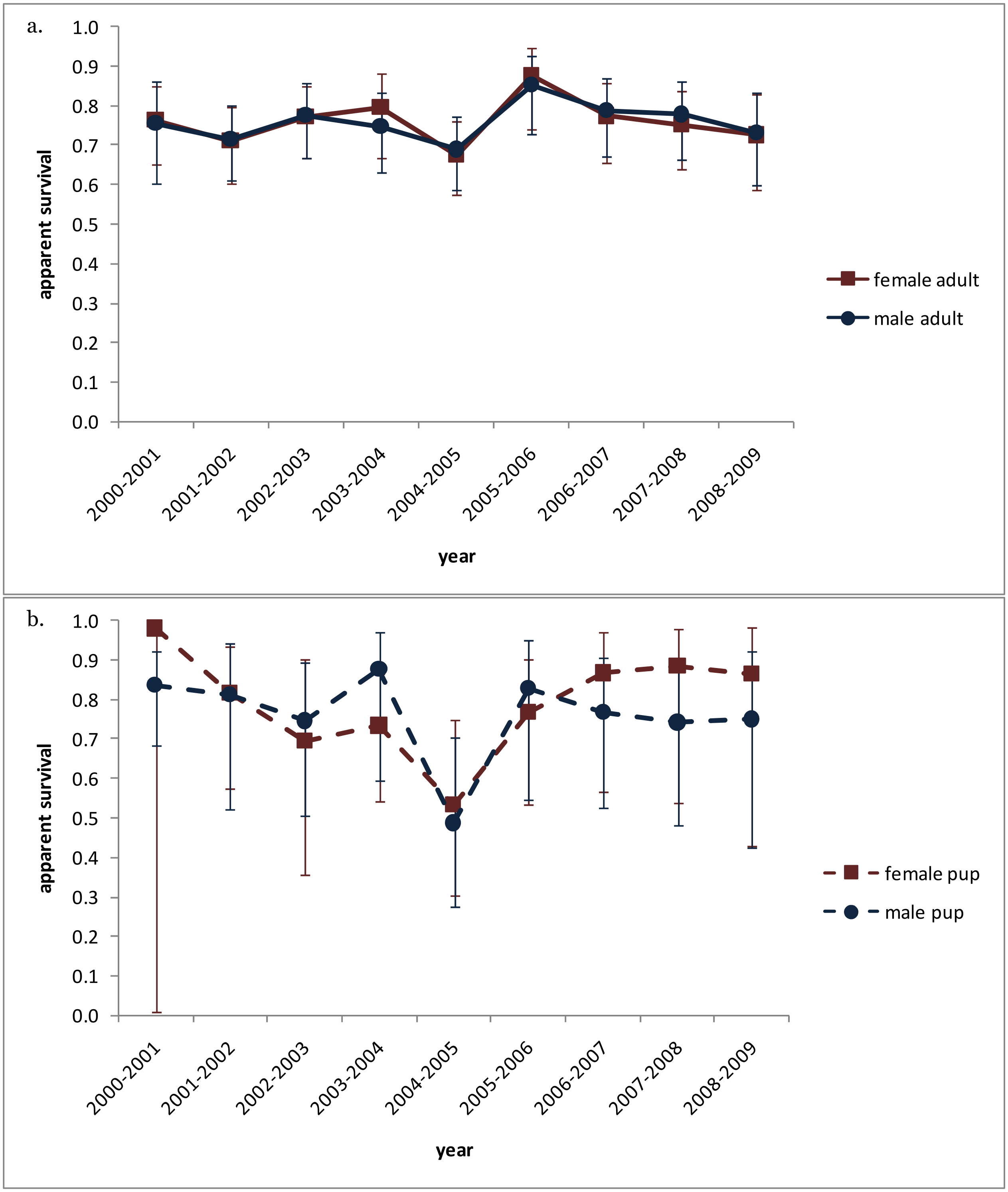


Fig. 9. Survivorship for (a) adult and (b) juvenile male and female foxes (all three trapping grids combined), 2000–2009, San Nicolas Island, California.

DISCUSSION

Notable findings from trapping efforts in 2009 were that 1) overall there was little change in the fox population over the island as a whole but that 2) the age structure and spatial distribution of foxes is changing, 3) different analyses of mark-recapture data yield different results for estimated population densities on the grids, 4)annual survival remains high in both juvenile and adult animals regardless of gender, 5)productivity was down on the west end 6) foxes were overall healthy, with low incidence of injury and 7) although there is no signal of an immediate threat of an epidemic, CAV and CDV continue to persist in the population and CPV has re-emerged in the fox population.

The number of foxes estimated from mark-recapture efforts on San Nicolas Island remained high in 2009, fueled by increases in the two western-most grids which offset a decline in Skyline grid. Capture success, number of adults captured and estimated population sizes were all up 2%-3% from 2008. Estimates of adult population size on the grids appear lower than reported in Garcelon and Hudgens (2009), because the latter mistakenly included pups in their MARK analyses. Pups were also mistakenly included in MARK analyses of adult population size in Garcelon and Hudgens (2007). The correct adult population size estimates are presented in figures 6-8. Long-term trends in population size on the three trapped grids are similar regardless of whether only adults or both adults and pups are considered (e.g., compare Fig. 5 with Figs. 6-8).

Age structure of the fox population depicts some interesting patterns across the three grids. Both Tuft's and Skyline grids had a lower percentage of foxes assigned to age class 1 compared to 2008 (decrease of 9% and 19%, respectively). This may be explained in part by the low number of pups detected on those grids in 2008. Only 3 pups were captured on the Tuft's grid and 4 on Skyline in 2008. While age class does not precisely track chronological age, if immigration of age class one animals does not occur then fewer pups produced on a grid may lead to changes in the age class structure. Redeye had 15 pups captured in 2008 and had the highest proportion of age class one individuals in 2009. The Tuft's grid has typically had the highest proportion of older age-class foxes, although in 2008 the proportion decreased on that grid and the Redeye grid increased to nearly the same proportion of age class 4 foxes. In 2009, Tuft's again had the highest proportion of older aged animals, although Redeye had the highest proportion of foxes in the eldest (age class 4) category.

The spatial distribution of foxes on the island appears to be shifting toward the west end. There was an east-west trend in population growth rates, increasing from a substantial population decline on Skyline grid (λ=0.67), to slight population growth on Tuft's grid (λ=1.05) and larger growth on Redeye grid (λ=1.17; but see below). This gradient could reflect a net dispersal from the east to the west end, or differences in demographic rates driven either by habitat differences or a gradient in human activity. Although we did not specifically look at grid-specific survival, the top model used to estimate population sizes on the grids was one in which annual apparent survival of adults captured on Skyline was lower than either Redeye or Tuft's animals. However, because apparent survival does not account for permanent emigration from a grid, this result is consistent with either hypothesis (i.e., high dispersal from east to west or low demographic rates in the east end compared to the west end).

Again this year we employed two different techniques to calculate fox density on the grids. The first is the method we have used for the previous nine years and is determined using two values; the population estimate derived from mark-recapture data using program MARK, and the effective trap area calculated using a formula which incorporates the movements of foxes during the trapping period (mean maximum distance moved - MMDM). Comparisons made on San Clemente Island between grid trapping-based density estimates (using MARK and MMDM buffers) and telemetry-based home range estimates found that the former resulted in a density that was biased high (Garcelon 1999, Schmidt *et al.* 2004). This appears to be associated with foxes moving shorter distances during the trapping period (likely due to the presence of food in the traps) and therefore the effective trap area is smaller than it should be to provide an accurate density estimate.

For the second year in a row we used an additional method to estimate fox density on the grids. Rather than using the conventional buffer strip around a trapping grid that is determined by the target animal's movements or home range size, program DENSITY (Efford et al. 2004) uses the locations where each animal is detected to fit

a spatial model of the detection process. As it is unbiased by "edge effects" or incomplete detection, it should provide a more accurate estimate of population density.

All of the density estimates derived from program DENSITY were lower than those calculated from the MARK/MMDM method. Estimates from program DENSITY were 57%, 84% and 34% lower than MARK/MMDM estimates for Redeye, Skyline and Tuft's, respectively. Using home ranges sizes determined by radio-telemetry for foxes on San Clemente Island, Schmidt et al. (2004) found that the MARK/MMDM method provided density estimates that were 19 – 55% higher than home range-based estimates. While similar telemetry data are not available for San Nicolas Island, if we assume similar behavioral response to trapping and comparable home range sizes, then the results from program DENSITY may be providing a more accurate estimate of fox density.

Estimates of population growth rates (λ) depended on what metric of population size was used to calculate them. Growth rates calculated from population density, as estimated from program DENSITY, were lower on both Skyline and Redeye grids and higher on Tuft's grid than were growth rates calculated from population size, as estimated from program MARK (Table 6 compared to Figs. 6b-8b). The discrepancy is particularly noticeable on the Redeye grid, where all population indices (i.e., capture success, # adults captured, MARK based population estimates) indicate a population increase from 2008 to 2009 (λ=1.17), while density estimates from program DENSITY were slightly lower in 2009 than in 2008 (λ=0.97). The lower density estimate reflects an increased effective trap area estimated for 2009 compared to 2008. It is not clear whether the increased effective trap area estimated for 2009 is due to increased home ranges for foxes, differences in movement behaviors associated with differences in adult reproductive status, or an artifact of higher capture success. Extremely high capture success at high densities could lead to higher probabilities that the trap which first captured a fox, and adjacent traps, were occupied by another animal on subsequent days. A fox would then have to travel further to encounter an unoccupied trap than it would if densities (and consequently capture success) were lower. This could potentially result in an apparent increase in its home-range size estimated from the spatially explicit mark-recapture analysis employed by program DENSITY. While program DENSITY has a great deal of promise as an unbiased estimator of fox densities on the grids, the influence of high fox densities on fox movement with respect to traps needs to be further examined before it is relied upon as the sole tool for estimating year-to-year changes in population size in high-density regions of the island.

Most of the foxes we examined appeared healthy. We found no indications infectious disease in the fox population. Many of the physical anomalies that were observed in captured foxes were consistent with intra-specific aggression, such as minor cuts and abrasions, torn lips and ear tissue injuries. Injuries associated with intra-specific aggression are not uncommon in island fox populations and would be expected, especially in areas of such high fox density. The majority of the foxes (~85%) examined were in good to very good physical condition. During the summer months foxes will generally be lean, as was the case for most examined, but for the San Nicolas population that still equated to "good" condition for most animals. The occurrence of ~15% of the animals considered to be in poor body condition is not uncommon, as both older individual and females that had recently completed lactation can tend to be in poor body condition.

Annual survival was similar in 2009 to that estimated for previous years, and did not differ between males and females or between adults or juveniles. We suggest that future analyses would have the greatest power to detect a drop in survival by combining males and females and comparing current year survival to the average survival from previous years. Although our analysis suggests that adult and juvenile survival could be lumped, we believe it remains worthwhile to analyze these groups separately as some threats to the fox population are more likely to strike pups than adults (e.g., CPV). Finally, we suggest that it would be worthwhile in future years to incorporate spatial differences (i.e., grid-specific analysis) into survivorship monitoring.

There were relatively few pups captured on the Tuft's and Redeye grids compared to most previous years, resulting in a fairly low adult female:pup ratio. For example, in 2007 and 2008 we captured 27 and 22 pups, respectively. Only 12 pups were captured in 2009. While an unknown percentage of the pups produced were undoubtedly not captured, the proportion of females showing signs of lactation was low (21% compared to 32% in 2008). Several factors may have contributed to low pup production on the

west-end grids. The majority of adults on Redeye grid were either age class 1 or age class 4. These two age classes are predominately foxes with relatively low reproductive output, yearlings or senescent adults, respectively. Although Tuft's grid had relatively few animals in these age classes, females captured there weighed on average 340 grams less than females on the other grids, which may reflect poorer nutritional state. Fox numbers were also the highest (Redeye) or second highest (Tuft's) on record. Only in 2002 were fox numbers greater on Tuft's; few pups were captured in that year as well (Fig. 5). High levels of intra-specific competition may have been exacerbated by relatively poor rainfall in winter/spring 2009.

Serology Testing

Virus exposure was assessed in 43 foxes via measurement of serum antibody levels to canine distemper (CDV), canine parvovirus (CPV) and canine adenovirus (CAV). Antibody levels are measured in serum and reported in terms of titers, or dilution at which antibodies can be detected. The higher the titer number, the more antibodies are present.

In 2008, the seroprevalence of CAV was 58% followed by the 49% observed in 2009. Clifford et al. (2006) reported that 40% of the SNI foxes had positive titers for CAV from samples collected in 2001-2003. The fluctuation in seroprevalence of CAV from between 40-58% over nearly a decade time suggests that CAV is enzootic and has a high rate of transmission within the fox population, similarly to what has been found in the Yellowstone wolf population (Almberg et al. 2009). It is lower than the 81% seroprevalence found in 2007 in the fox population on San Clemente Island (Garcelon et al. 2008). One fox had a titer >=12288 (Appendix C), suggesting recent exposure or possibly being actively infected with CAV. CAV-1 is spread through nasal discharge and urine, and gets into the body via the oral cavity or through inhalation. It produces infectious canine hepatitis, which can cause inflammation of the liver. There has been no evidence of disease in the SNI fox population attributed to this pathogen, but continued surveillance is merited.

We found measurable CDV titers in 7% of the foxes tested. This is an order of magnitude lower than the seroprevlence found for CDV on SNI in 2008 (70%; Garcelon and Hudgens 2009). It is also lower than the 32.8% ("definite positive") and 41.8% ("suspect positive) found by Clifford et al. (2006) from serum samples collected in 2001-2003. It is possible that the presence of "protected" foxes from previous vaccination efforts has interrupted the transmission of the native CDV virus and reduced the overall seroprevalence in the SNI foxes. As we still know little about the natural fluctuation in CDV antibody in fox populations, it is also possible that either the virus was at a naturally low prevalence in 2009 or that the lower rates are due to sampling artifacts. Continued effort to monitor the serology of the SNI fox population and making comparisons with other island fox populations should help address these questions.

A relatively small proportion of the sampled foxes had titers positive for exposure to CPV. As no positive results were obtained in 2008, the 7 (16%) positive samples indicates that either that this pathogen was overlooked or has re-emerged in the San Nicolas Island fox population. The probability that none of the 50 foxes sampled in 2008 had CPV, if the pathogen was present in the population at levels observed in 2007 (6%) or 2009 (16%), is between 0.0001 and 0.05. This suggests that if CPV was present on SNI in 2008, it was at very low prevalence.

CONCLUSIONS AND RECOMMENDATIONS

The largest risk currently facing San Nicolas Island foxes is the potential for an introduced disease to quickly decimate the population. San Nicolas Island foxes currently have two risk factors promoting susceptibility to an introduced disease. First, the sustained high density of foxes on the island represents a risk factor, as the persistence and spread of disease throughout a population is closely tied to population density (Anderson and May 1981, Finkenstadt and Grenfell 1998). San Nicolas Island foxes face a further risk since the population has extremely low genetic diversity, (Aguilar *et al.* 2004); although they do report relatively high diversity in MHC genes

which are closely associated with immune responses. Low genetic diversity can be associated with reduced disease resistance, increased risk severity and length of disease epidemics in populations (Sprinbett *et al.* 2003). Levels of genetic diversity observed in San Nicolas Island foxes are caused by severe population bottlenecks leading to high levels of inbreeding. Such inbreeding is also associated with increased susceptibility to disease and environmental extremes (Keller and Waller 2002).

In order to reduce the risk of catastrophic disease, we incorporated a vaccination program associated with our trapping efforts. A large percentage of the animals caught were given canine distemper and rabies vaccinations. Modeling work by V. Baker and D. Doak (personal communication) has shown that, if the vaccinations are highly effective, this type of vaccination program is the most effective way of preventing an epidemic of those diseases. This vaccination program does not, however, provide any protection from potential disease threats other than canine distemper and rabies, and may not protect against all strains. Future monitoring of disease prevalence should prioritize unvaccinated animals on grids, but should include grid animals vaccinated against CDV so that spatial differences of CAV and CPV prevalence can be evaluated in the context of changes in demographic rates and population size on the grids. We also advocate within-year monitoring of fox survival, as demonstrated from 2006-2008 using an automated survival monitoring system (Hudgens et al. 2007, 2008), to provide for early detection of lethal disease outbreaks. Part of this monitoring program should include developing specific triggers, based on types and frequency of mortalities, to further management actions (Hudgens et al. 2007, 2008). This type of monitoring system, in conjunction with prophylactic vaccination of a subset of foxes for canine distemper and rabies virus, may help prevent the catastrophic decline of the fox population should one of these disease agents be introduced to the population.

We also advocate building a better understanding of San Nicolas Island fox feeding and breeding ecology to address two questions. First, what is the role of introduced species in maintaining high fox densities on San Nicolas Island? Understanding whether these resources act to promote longevity, reproduction, or buffer populations from environmental variation will allow predictions of the continued spread or control of these species on San Nicolas Island will impact foxes. Secondly, how does breeding potential change with fox age? Understanding which foxes contribute the most to pup production will help to elucidate whether some areas of the island act as population sinks (or sources). More importantly, such an understanding will provide information about mechanisms that maintain high fox densities but do not contribute to future fox generations. The answer to both questions will be necessary to make good predictions about how management of introduced food resources will impact foxes. Being able to separate and understand the roles of introduced species, and other island resources, in maintaining high population densities and contributing to future fox generations will allow the Navy to effectively manage these species without risking endangering San Nicolas Island foxes.

REFERENCES

Aguilar, A., G. Roemer, S. Debenham, M. Binns, D. Garcelon, and R. K. Wayne. 2004. High MHC diversity maintained by balancing selection in an otherwise genetically monomorphic mammal. Proceedings of the National Academy of Sciences 101: 3490–3494.

Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. In Second International Symposiumon Information Theory (Petrov, B.N. and Csaki, F., eds), pp. 267–281, Akademiai Kiado.

Almberg, E.S., L.D. Mech, D.W. Smith, J.W. Sheldon, R.L. Crabtree. 2009. A serological survey of infectious disease in Yellowstone National Park's canid community. PLoS ONE 4(9):e7042.doi:10.1371/journal.pone.0007042.

Anderson, R. M., and R. M. May. 1981. The population dynamics of microparasites and their invertebrate hosts. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences. 291:451–524.

California Department of Fish and Game. 1987. Five-year status report on the island fox (*Urocyon littoralis*). Unpublished report, California Department of Fish and Game, Sacramento, California. 7pp.

Clifford, D.L., J.A.K. Mazet, E.J. Dubovi, D.K. Garcelon, T.J. Coonan, P.A. Conrad and L. Munson. 2006. Pathogen exposure in endangered island fox (*Urocyon littoralis*) populations: implications for conservation management. Biological Conservation 131: 230-243.

Collins, P. W. 1982. Origin and differentiation of the island fox: a study of evolution in insular populations. M. A. thesis, University of California, Santa Barbara. 303pp.

Collins, P. W. 1993. Taxonomic and biogeographic relationships of the island fox (*Urocyon littoralis*) and gray fox (*U. cinereoargenteus*) from Western North America. Pages 351–390 *in* F. G. Hochberg, editor. Third California Islands Symposium: Recent advances in research on the California Islands, Santa Barbara Museum of Natural History, Santa Barbara, California.

Efford, M.G., D.K. Dawson and C.S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27.1: 217-228.

Finkenstadt, B., and B. Grenfell. 1998. Empirical determinants of measles metapopulation dynamics in England and Wales. 265:211–220.

Garcelon, D. K. 1999. Island fox population analysis and management recommendations. Unpublished Report submitted to: Southwest Div., Naval Fac. Eng. Command, San Diego, California. 57pp.

Garcelon, D. K., and G. A. Schmidt. 2005. Island Fox Monitoring and Demography on San Nicolas Island–2004. Unpublished report prepared by the Institute for Wildlife Studies, Arcata, California. 24pp.

Garcelon, D. K., L. Munson, T.W. Vickers and D. Simmons. 2008. Research study on the pathology and veterinary services for island foxes on San Clemente Island. Final report under agreement N62473-06-LT-R0057, Naval Facilities Engineering Command, Southwest, San Diego, CA. 8 pages + Appendices.

Gilbert, D. A., N. Lehman, S. J. O'Brien, and R. K. Wayne. 1990. Genetic fingerprinting reflects population differentiation in the California Channel Island fox. Nature 344:764–767.

Goldstein, D. B., G. W. Roemer, D. A. Smith, D. E. Reich, A. Bergman, and R. K. Wayne. 1999. The use of microsatellite variation to infer patterns of migration, population structure, and demographic history: An evaluation of methods in a natural model system. Genetics 151:797–801.

Hall, E. R. 1981. The mammals of North America, 2nd ed. John Wiley and Sons, New York.

Halverson, W. L., S. Junak, C. Schwemm, and T. Keeney. 1996. Plant communities of San Nicolas Island, California. Technical Report No. 55. National Biological Service, University of Arizona, Tucson, Arizona.

Hudgens, B., F. Ferrara, and D. Garcelon. 2007. Remote monitoring of island foxes. Report to DoD Legacy Program, May 2007. 13pp.

Hudgens, B., F. Ferrara, and D. Garcelon. 2008. Digital radio-telemetry monitoring of San Nicolas Island foxes. Report to DoD Legacy Program, May 2007. 19pp.

Johnson, J. B., and K. S. Omland. 2003. Model selection in ecology and evolution. Trends Ecol. Evol. 19:101–108.

Juola F. A., G. A. Schmidt, P. B. Sharpe, and D. K. Garcelon. 2002. Island Fox Monitoring and Demography on San Nicolas Island–2001. Unpublished report *prepared by* the Institute for Wildlife Studies, Arcata, California. 34pp.

Keller L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. TRENDS in Ecology and Evolution 17:230–241.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the Robust Design. Biometrics 51:293–308.

Kendall, W. L. 2001. The Robust Design for capture-recapture studies: analysis using program MARK. Pages 357–360 in Proceedings of the 2nd International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA.

Kohlmann, S. G., G. A. Schmidt, R. C. Wolstenholme, and D. K. Garcelon. 2003. Island fox recovery efforts on Santa Catalina Island, California, October 2001–October 2002, Annual Report. Unpublished report by the Institute for Wildlife Studies, Arcata, California for the Ecological Restoration Department, Santa Catalina Island Conservancy, Avalon, California. 83pp.

Kohlmann, S. G., G. A. Schmidt, and D. K. Garcelon. 2005. A population viability analysis for the Island Fox on Santa Catalina Island, California. Ecological Modeling 183:77–94.

Moore, C. M., and P. W. Collins. 1995. *Urocyon littoralis*. Mammalian Species, No. 489. 7pp.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

Pollock, K. H., J. D. Nichols, J. E. Hines, and C. Brownie. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107.

Roemer, G. W., D. K. Garcelon, T. J. Coonan, and C. Schwemm. 1994. The use of capture-recapture methods for estimating, monitoring, and conserving island fox populations. Pages 387–400 in W. L. Halverson and G. J. Maender, editors. The Fourth California Channel Islands Symposium: Update on the Status of Resources. Santa Barbara Museum of Natural History, Santa Barbara, California.

Roemer, G. W., T. J. Coonan, D. K. Garcelon, J. Bascompte, and L. Laughrin. 2001. Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Animal Conservation 4:307–318.

Schmidt, G. A., and D. K. Garcelon. 2003. Island Fox Monitoring and Demography on San Nicolas Island–2002. Unpublished report *prepared by* the Institute for Wildlife Studies, Arcata, California. 22pp.

Schmidt, G. A., and D. K. Garcelon. 2004. Island Fox Monitoring and Demography on San Nicolas Island–2003. Unpublished report *prepared by* the Institute for Wildlife Studies, Arcata, California. 24pp.

Schmidt, G. A., B. Willson, and D. K. Garcelon. 2004. Island fox monitoring and research on Naval Auxiliary Landing Field, San Clemente Island, California. Unpublished report *prepared by* the Institute for Wildlife Studies, Arcata, California. 63pp.

Schmidt, G. A., B. R. Hudgens, and D. K. Garcelon. 2007. Island Fox Monitoring and Demography on San Nicolas Island–2006. Unpublished report *prepared by* the Institute for Wildlife Studies, Arcata, California. 26pp.

Schmidt, G. A., B. R. Hudgens, and D. K. Garcelon. 2006. Island Fox Monitoring and Demography on San Nicolas Island–2005. Unpublished report *prepared by* the Institute for Wildlife Studies, Arcata, California. 24pp.

Springbett, A. J., K. MacKenzie, J. A., Woolliams, and S. C. Bishop. 2003. The contribution of genetic diversity to the spread of infectious diseases in livestock populations. Genetics 165:1465–1474.

Suckling. K., and D. K. Garcelon. 2000. Petition to list four island fox subspecies as endangered species. Formal petition to list the San Miguel Island fox (*Urocyon littoralis littoralis*), Santa Rosa Island fox (*U. l. santarosae*), Santa Cruz Island fox (*U. l. santacruzae*), and the Santa Catalina Island fox (*U. l. catalinae*) as “endangered” throughout their range. *Prepared by* the Center for Biological Diversity, Tucson, Arizona and the Institute for Wildlife Studies, Arcata, California *for* the United States Department of the Interior and the United States Fish and Wildlife Service. 24pp.

Timm, S. F., J. M. Stokely, T. B. Gehr, R. L. Peebles, and D. K. Garcelon. 2000. Investigation into the decline of island foxes on Santa Catalina Island. Unpublished report *prepared by* the Institute for Wildlife Studies *for* the Ecological Restoration Department, Santa Catalina Island Conservancy, Avalon, California. 32pp.

Wayne, R. K., S. B. George, D. Gilbert, P. W. Collins, S. D. Kovach, D. Girman, and N. Lehman. 1991. A morphologic and genetic study of the island fox, *Urocyon littoralis*. Evolution 45:1849–1868.

White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement 120–138.

Wilson, D. E., and D. M. Reeder. 1993. Mammal species of the World: a taxonomic and geographic reference, 2nd ed. Smithsonian Institution Press, Washington, DC.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13–21.

Wood, J. E. 1958. Age structure and productivity of a gray fox population. Journal of Mammalogy 39:74–86.

ACKNOWLEDGMENTS

This report was funded by the NAWCWD and the Department of the Navy under the administration of the Naval Facilities Engineering Command, Southwest, San Diego, California. We give special thanks to Grace Smith, SNI Natural Resources Manager, for her logistical support and valuable assistance to this project in a variety of ways. Gina Smith contributed logistical support on San Nicolas Island. We thank IWS employees Hower Blair, Kari Signor, Daniel Jackson, Thomas Thein, Julie Young and Jessica Sanchez for their assistance with the fieldwork.

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APPENDIX A

Island fox demography grids showing trap numbers and locations, San Nicolas Island, California.

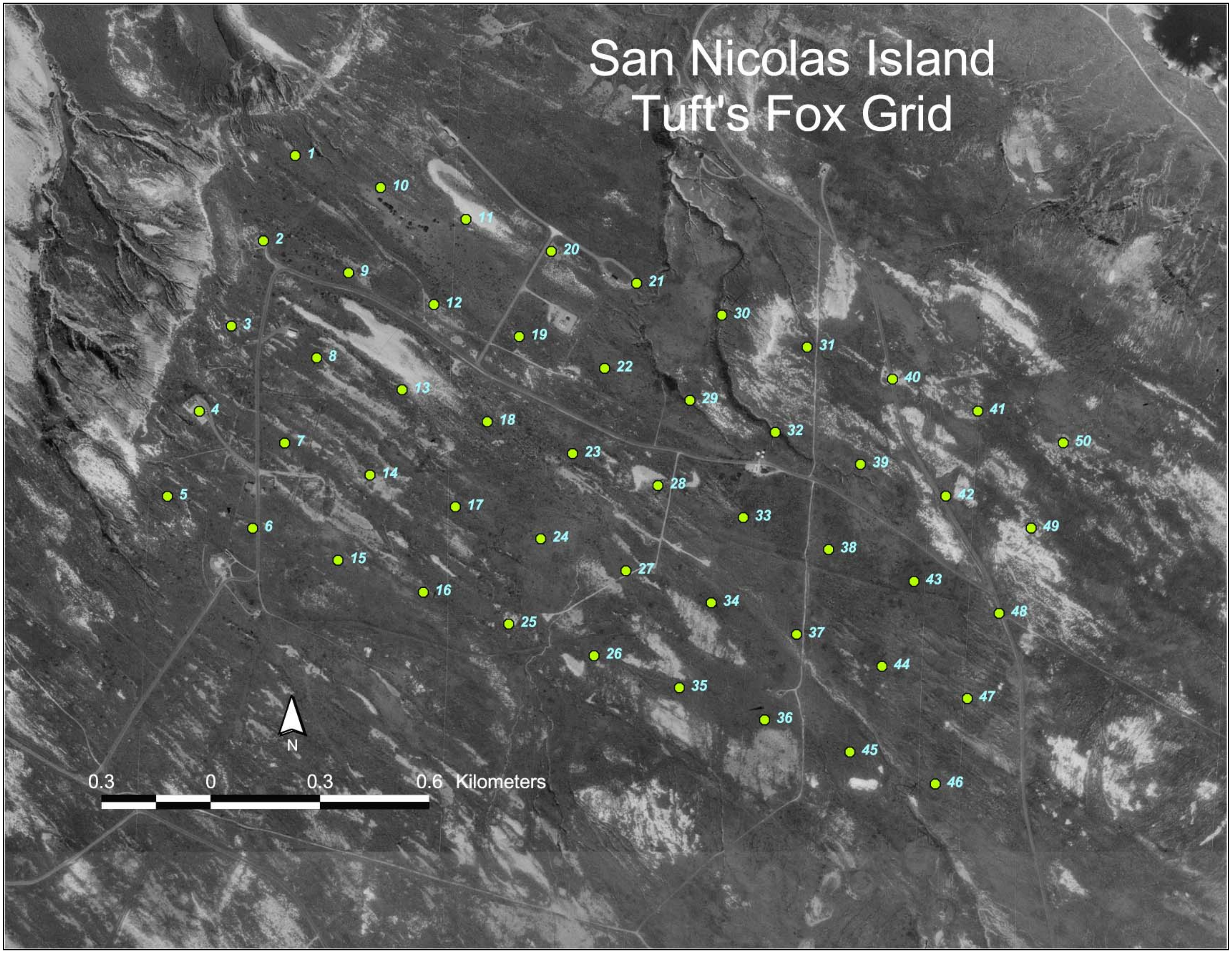

Figure A-1. Tuft's island fox demography grid, San Nicolas Island, California.

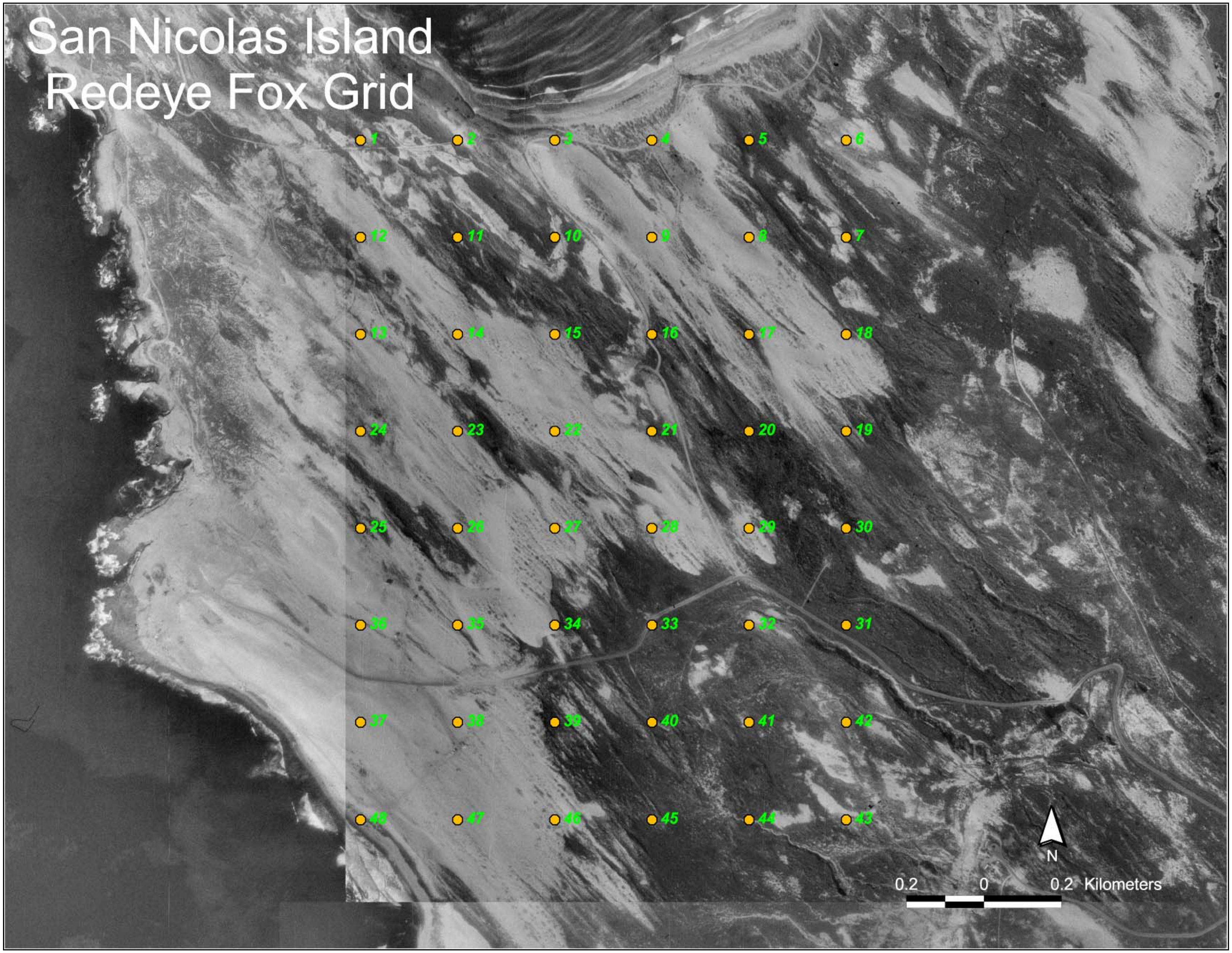

Figure A-2. Redeye island fox demography grid, San Nicolas Island, California.

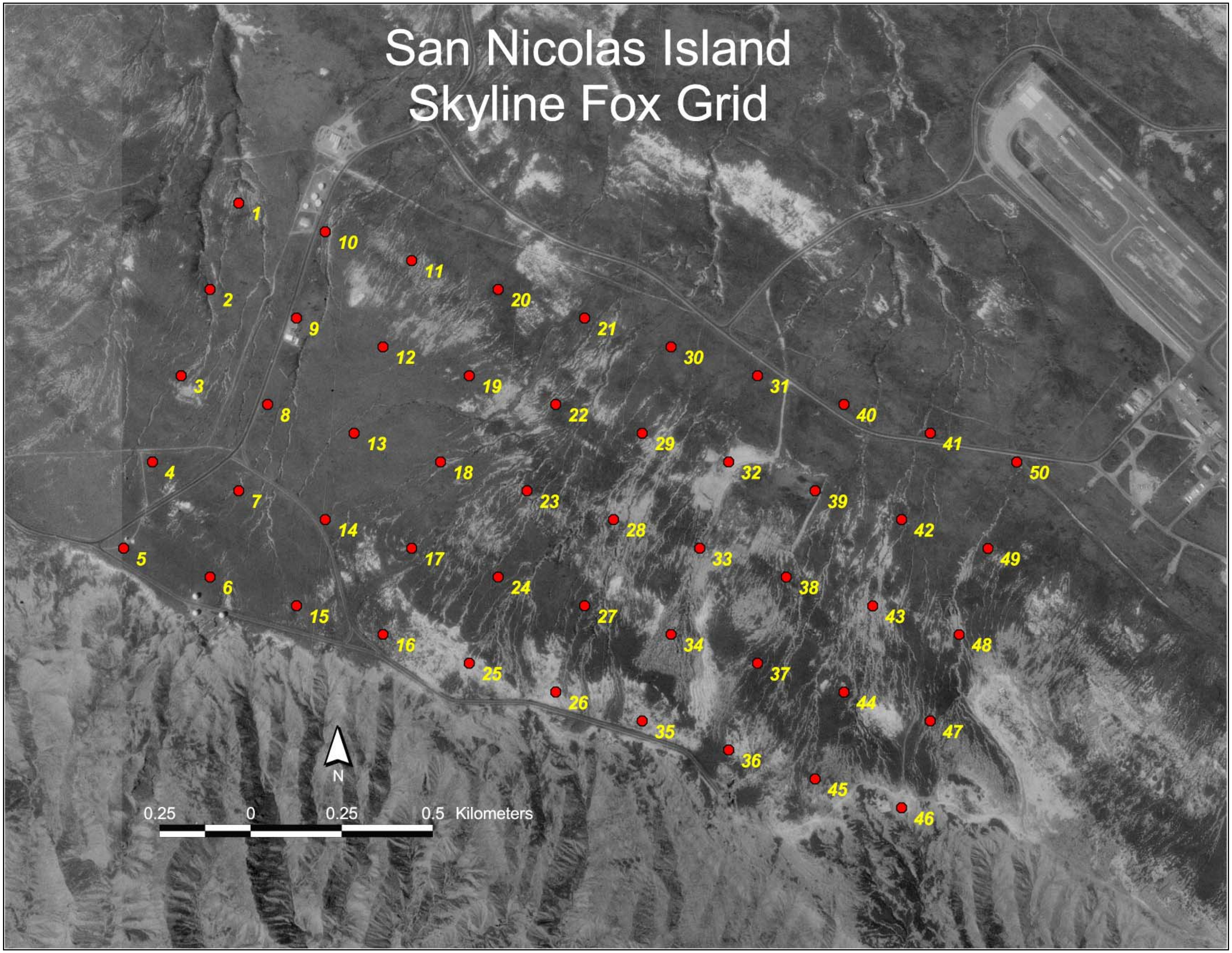

Figure A-3. Skyline island fox demography grid, San Nicolas Island, California.

APPENDIX B

Relationship between age class and true age of known age foxes captured between 2000 and 2009.

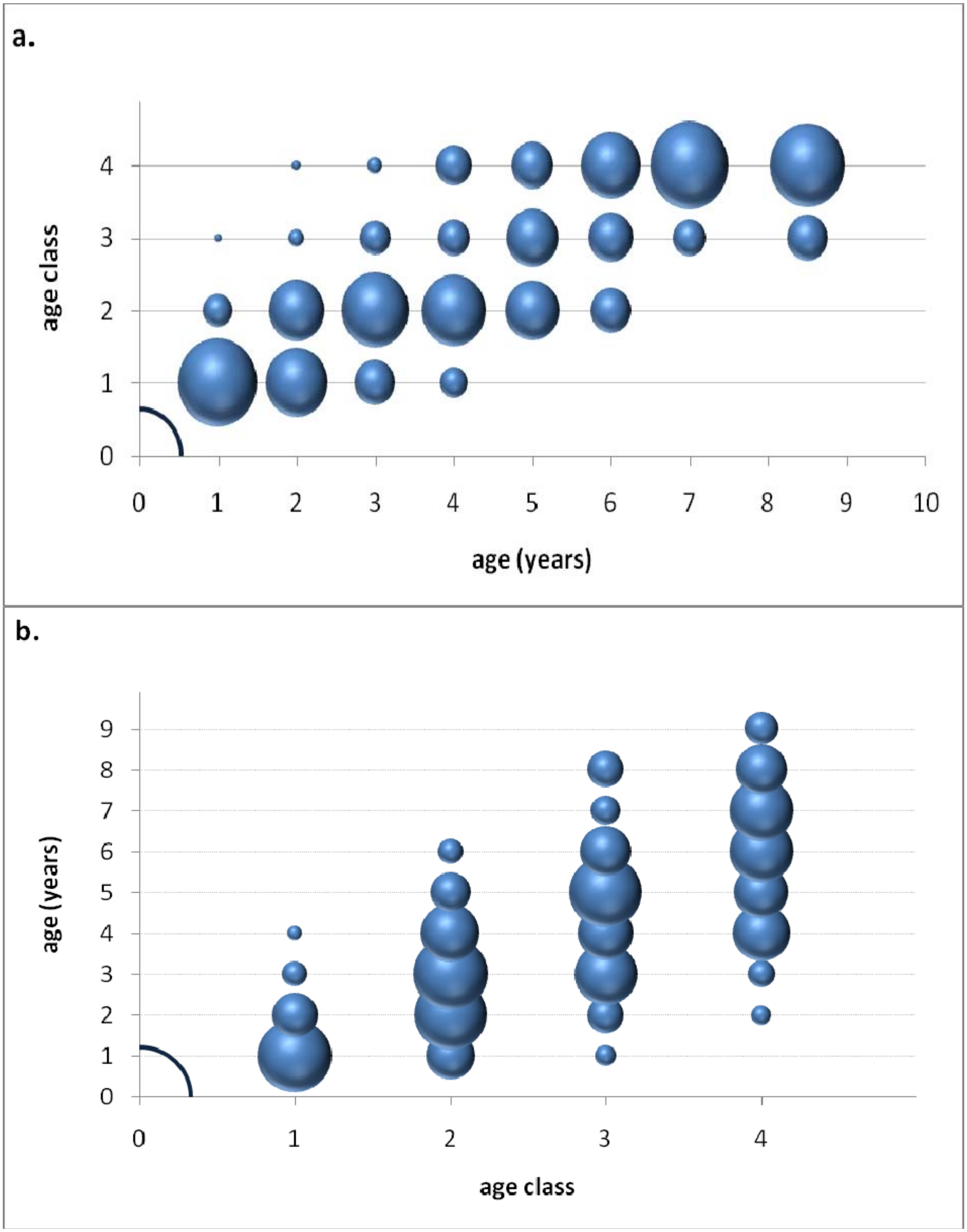

Figure B1. Relationship between age class and true age of known age foxes captured on San Nicolas Island, California between 2000 and 2009. Size of the bubbles indicates the proportion of a) foxes of a given age (x-axis) assigned to the age class on the y-axis or b) foxes assigned to a given age class (x-axis) that were the age indicated on the y-axis. Quarter circle in the lower left corner of both panels represent pups, which were assumed to have been assigned with 100% accuracy.

APPENDIX C

Serum titers for canine adenovirus, canine distemper virus, and canine parvovirus from blood samples collected on San Nicolas Island in 2009.

Fox ID	CAV	CDV	CPV
15E22	<4	<4	40
24433	1024	<4	<20
25F28	<4	<4	<20
3027B	>= 12288	<4	<20
33915	32	<8	20
36564	6	<4	<20
44246	6144	<8	<20
50924	<4	<4	<20
60833	<4	<8	<20
7280F	<4	<4	<20
76906	6144	<4	<20
76A0D	<4	<8	<20
80A59	1536	<8	<20
82211	<4	<8	<20
82A1A	4	<8	<20
82C6A	<4	<8	<20
B0A19	<4	<8	<20
D0C16	<4	<8	<20
D247B	<4	<4	<20
D682E	<4	<8	<20
E6832	4096	<4	<20
F4C71	3072	<8	<20
05B74	<4	<4	20
11C78	<4	<4	<20
7203F	<4	<4	<20
95963	3072	4	<20
A3248	6	6	<20
B1B0B	<4	<4	<20
C3F40	3072	<4	20
C7A2C	<4	<4	<20
E016B	<4	<4	20
83C23	768	<4	20
50C2F	4096	<4	20
252CD	4096	48	<20
73C4F	1024	<8	<20
2E941	<4	<8	<20
24B11	<4	<16	<20
62F29	1536	<16	<20
06D32	<4	<4	<20
33078	1024	<8	<20
71817	512	<4	<20
A360A	<4	<4	<20
D7576	12	<4	<20